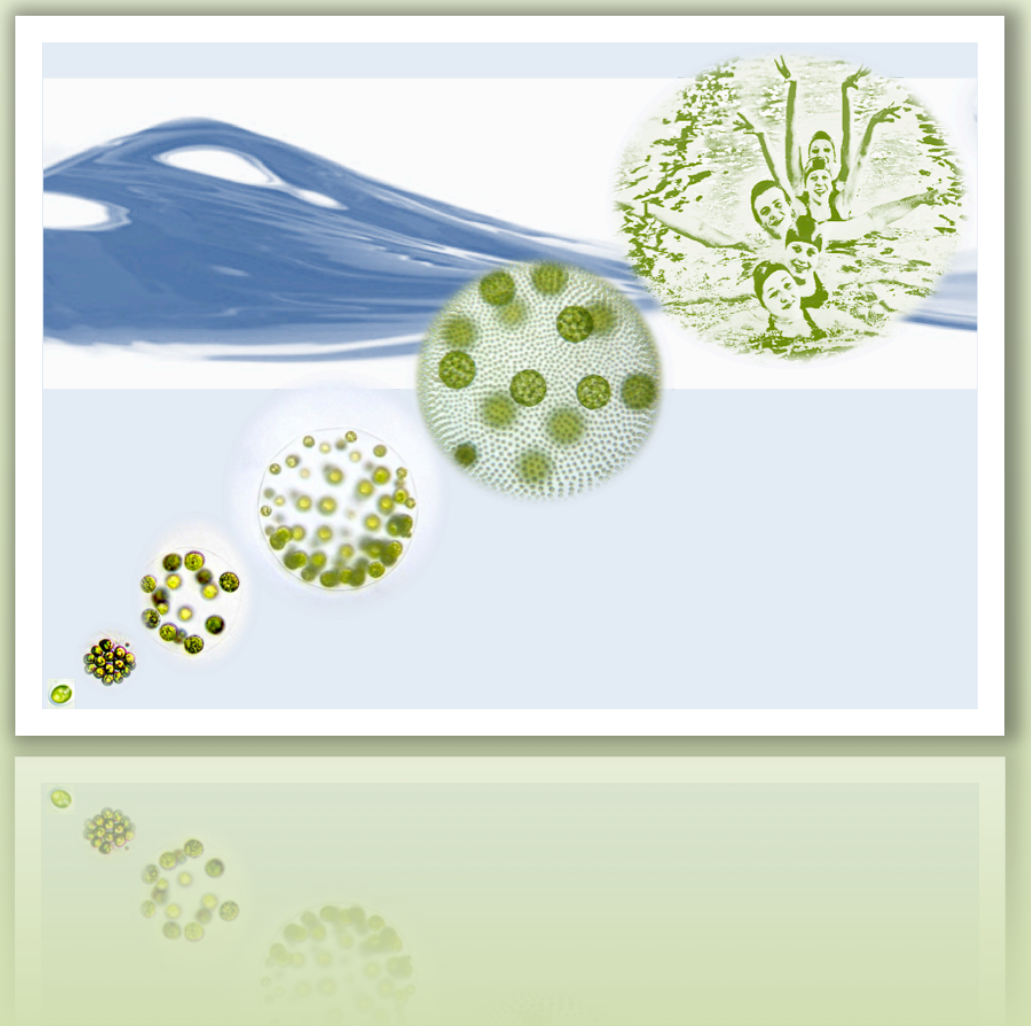
THE 1st INTERNATIONAL VOLVOX CONFERENCE

December 1 – 4, 2011

Biosphere 2, Arizona, USA



SCOPE

This is the first (http://www.unbf.ca/vip/IVC/index.htm) of what we hope to be a long series of *Volvox* meetings to be held every other year, alternating with the Chlamy meeting. The idea of a meeting on everything about *Volvox* and its relatives (aka Volvocales or volvocine algae) reflects both an increase in the size of the *Volvox* community and the realization that many researchers from fields traditionally not associated with *Volvox* research (e.g., physics, theoretical biology) are interested in various aspects of the system. Indeed, volvocine algae have become an important model system for the evolution of multicellularity, development and cellular differentiation, and lately have yielded important results in fields as diverse as genomics, hydrodynamics, and social evolution. We hope that such a meeting will foster exchange of ideas and expertise, and will initiate new collaborations. Furthermore, with these meetings we wish to attract new people and to build a stronger *Volvox* community.

CONFERENCE ORGANIZER

Aurora M. Nedelcu, University of New Brunswick, Canada

ORGANIZING COMMITTEE

Annette Coleman, Brown University, USA
Armin Hallmann, University of Bielefeld, Germany
Matthew Herron, University of British Columbia, Canada
Stephen Miller, University of Maryland Baltimore County, USA
Hisayoshi Nozaki, University of Tokyo, Japan
Simon Prochnik, Joint Genome Institute, USA
Deborah Shelton, University of Arizona, USA
James Umen, Donald Danforth Plant Science Center, USA

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PROGRAM AT A GLANCE

Day	Time	Activity	Location
December 1st			
	4:00 - 5:30	Registration	Biosphere 2 LOBBY
	5:00 - 6:30	Welcome remarks and social mixer	SAHARA Room
	6:30 – 8:30	Dinner	SAHARA Room
December 2nd			
	7:30 – 8:30	Breakfast	B2 CAFÉ
	8:30 – 10:00	Morning Session 1: Life Cycle	SONORAN Room
	10:00 – 10:30	Break	Patio
	10:30 – 12:00	Morning Session 2: Development	SONORAN Room
	12:00 – 1:30	Lunch	PATAGONIA Room
	1:30 – 2:45	Afternoon Session 1: Physics	SONORAN Room
	2:45 – 3:15	Break	Patio
	3:15 – 4:30	Afternoon Session 2: Evolution	SONORAN Room
	5:00 – 6:30	Poster Session	MOJAVE room
	6:30 – 8:30	Dinner	PATAGONIA Room
December 3rd			
	7:30 – 8:30	Breakfast	B2 CAFÉ
	8:30 – 10:10	Morning Session 1: Genomics	SONORAN Room
	10:10 – 10:30	Break	Patio
	10:30 – 12:10	Morning Session 2: Genetics	SONORAN Room
	12:10 – 1:30	Lunch	PATAGONIA Room
	1:30 – 2:45	Afternoon session 1: Workshop	SONORAN Room
	2:45 – 3:00	Break	Patio
	3:00 – 4:00	Afternoon Session 1: Workshop	SONORAN Room
	4:00 – 4:15	Break	
	4:15 – 5:05	Afternoon Session 2: Taxonomy	SONORAN Room
	5:30 – 6:30	Movie and Trivia Night	SAHARA Room
	6:30 – 9:00	Banquet	SAHARA Room
December 4th			
	7:30 – 8:30	Breakfast	B2 CAFÉ
	9:00 – 10:30	Tour of Biosphere 2	
	10:30 – 11:00	Break	Casita #500
	11:00 – 12:00	Round Table	CASITA #500
	12:00 – 1:30	Lunch (boxed)	Casita #500
	2:00	Leaving Biosphere	

SCIENTIFIC PROGRAM

FRIDAY, DECEMBER 2, 2011

MORNING SESSION 1: LIFE CYCLE (Chair: Annette Coleman)

8:30 – 8:45 **Introduction**

8:45 – 9:10 **Deborah Shelton** (University of Arizona)
Colonial reproduction and cell cycle regulation in volvocine algae

9:10 – 9:35 **Takashi Hamaji** (Kyoto University)
Mating type locus of *Gonium pectorale*

9:35 – 10:00 **Rintaro Hiraide** (University of Tokyo)
Mat3 divergence after the evolution of anisogamy in the colonial volvocales

MORNING SESSION 2: DEVELOPMENT AND CELL DIFFERENTIATION (Chair: Steve Miller)

10:30 – 10:45 **Introduction**

10:45 – 11:10 **Alicia D. Howard** (University of Maryland Baltimore County)
Establishment of a *Volvox* chromatin immunoprecipitation (ChIP) platform to analyze the function of the master cell-fate determination regulator RegA

11:10 – 11:35 **Arash Kianianmomeni** (Humboldt-University of Berlin)
Light receptors of *Volvox carteri*

11:35 – 12:00 **Oana Marcu** (NASA Ames Research Center & SETI Institute)
Elemental mapping of *Volvox* during oxidative stress

AFTERNOON SESSION 1: THE PHYSICS OF BEING MULTICELLULAR (Chair: John Kessler)

1:30 – 1:55 **John O. Kessler** (University of Arizona)
Why motility?

1:55 – 2:20 **Knut Drescher** (University of Cambridge & Princeton Univ)
The fidelity of phototaxis in *Volvox carteri*

2:20 – 2:45 **Cristian A. Solari** (Universidad de Buenos Aires)
A general allometric and life-history model for the transition to multicellularity and cellular differentiation

AFTERNOON SESSION 2: EVOLUTION (Chair: Matthew Herron)

3:15 – 3:40 **Aurora M. Nedelcu** (University of New Brunswick)
Evo-Volvo: Using the volvocine algae to address evolutionary questions

3:40 – 4:05 **Sergey Gavrilets** (University of Tennessee)
Rapid transition towards the division of labor via evolution of developmental plasticity

4:05 – 4:30 **Matthew D. Herron** (University of British Columbia)
Complexity and individuality in the volvocine algae

EVENING (5:00 – 6:30): POSTER SESSION

P1: Stephanie Hoehn (Bielefeld University)
Embryonic inversion in volvocine algae

P2: Aurelia R. Honerkamp-Smith (University of Cambridge)
Mechanical aspects of inversion in *Volvox carteri*

P3: Noriko Ueki (University of Bielefeld)
Phototaxis in the multicellular green alga *Volvox*

P4: Jose Ortega (University of Maryland Baltimore County)
Analysis of VARL domain equivalency among the RegA-group VARL proteins

P5: Vanina J. Galzenati (Universidad de Buenos Aires)
Abundance variation of Volvocales in response to temperature change

P6: Alexandra Y. Harryman (University of Maryland Baltimore County)
Developmental response of *V. carteri* to nutrient deprivation

P7: Richard E. Michod (University of Arizona)
Evolution of multicellularity and individuality in the volvocine green algae

P8: Qike Li (University of Arizona)
regA gene cloning from several *Volvox* species and characterization of *regA* in a *Volvox carteri weismannia regA*$^-$ mutant

P9: Richard E. Michod (University of Arizona)
regA Cooperation and conflict in the evolution of complexity

P10: Deborah Shelton (University of Arizona)
Cell-type allocation and variability in diverse *Volvox* species

SATURDAY, DECEMBER 3, 2011

MORNING SESSION 1: GENOMICS (Chair: Bradley JSC Olson)

8:30 – 8:55 **Simon Prochnik** (DOE Joint Genome Institute)
The *Volvox* genome provides insights into evolutionary strategies for evolving complexity

8:55 – 9:20 **Bradley J.S.C. Olson** (Kansas State University)
The Volvocales Genome Project

9:20 – 9:45 **David Roy Smith** (University of British Columbia)
Volvocalean organelle genome evolution

9:45 – 10:10 **Sa Geng** (Donald Danforth Plant Science Center)
Next generation transcriptome sequencing provides insights into the genetic control program for sexual differentiation in *Volvox carteri*

MORNING SESSION 2: MOLECULAR AND EVOLUTIONARY GENETICS (Chair: James Umen)

10:30 – 10:55 **James Umen** (Donald Danforth Plant Science Center)
The population genetics of *MT*: resolving the divergence paradox between *Chlamydomonas* and *Volvox MT* genes

10:55 – 11:20 **Patrick Ferris** (University of Arizona)
Elucidating the origins of the *regA* gene

11:20 – 11:45 **Erik R. Hanschen** (University of Arizona)
A Broader Look at the Origin of the VARL gene family

11:45 – 12:10 **Stephan G. Koenig** (University of New Brunswick)
New insights into the regulation of *regA* expression in *Volvox carteri*

AFTERNOON SESSION 1: WORKSHOP

1:30 – 4:00 Genome data analysis – approaches and challenges (Chair: Simon Prochnik)

1. The new *Volvox* (v2) and *Chlamydomonas* (v5) genome assemblies
2. Improved gene models with deep sequencing of mRNAs
3. Mapping existing gene names, deflines and descriptions to new annotations
4. The Phytozome Portal I: browsing gene models and supporting evidence; searching and analysis

2:45 – 3:00 Break

5. Phytozome II: tour of comparative plant and algal genomics tools at the Phytozome portal
6. Working with comparative genomics data to generate candidate gene lists and validate them experimentally
7. Future comparative genomics possibilities from the Volvocales genomes

AFTERNOON SESSION 2: TAXONOMY AND PHYLOGENY (Chair: Hisayoshi Nozaki)

4:15 – 4:40 **Hisayoshi Nozaki** (University of Tokyo)
New volvocacean algae progressively identified

4:40 – 5:05 **Y. Yang** (University of Tokyo)
Cryptic non-green endosymbiosis in the secondary photosynthetic eukaryotes, Chlorarachniophyta, based on extended phylogenetic analyses

EVENING SESSION

5:30 – 6:30 Movie and trivia night – Movies featuring volvocine algae

SUNDAY, DECEMBER 4, 2011

9:00 – 10:30 Tour of Biosphere 2

11:00- 12:00 Round Table: *Volvox* in the future (Discussion on ways to strengthen the *Volvox* community; establishing common resources – culture collection, genetic resources; student exchange programs; next *Volvox* meeting)

2:00 pm – Conference ends

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ABSTRACTS

TALKS (by session)

Life Cycle (Chair: Annette Coleman)

COLONIAL REPRODUCTION AND CELL CYCLE REGULATION IN VOLVOCINE ALGAE

Deborah Shelton
Dept. of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA

A life cycle consists of patterns of growth, division, and separation of cells. In unicellular species, these cell-level processes are typically regulated and deployed to maximize cell-level fitness. After an evolutionary transition to multicellularity, these same cell-level processes are presumably regulated so as to maximize colony-level fitness. Using the volvocine algae as a model system, we are investigating how the regulation of cell growth, division, and separation changes as a multicellular life cycle emerges. One fundamental aspect of cell cycle regulation in volvocine algae is the number of divisions per instance of multiple fission, *n*. In unicellular species, *n* is fecundity. In colonial species, *n* is both fecundity and colony cell number—a colony-level feature with potential effects on colony growth and viability. The fitness effects of regulating *n* in a particular way could be substantially different for unicellular compared to colonial species, and indeed "genetic modulation of cell number" has been proposed as an early step in the volvocine transition to multicellularity. However, there is little basic knowledge on patterns of regulation of *n* in simple colonial genera such as *Basichlamys* and *Gonium*. We think that such patterns should form the basis for detailed hypotheses concerning changes in cell cycle regulation during a major evolutionary transition. We are quantifying the relationship between *n* and parental cell size for a variety of relatively "simple" colonial Volvocales. We use a variety of culturing conditions to create parental cell size variation and light microscopy to assay the size of parental cells and number of offspring cells. These data complement a mathematical modeling approach designed to explore the ways in which growth, division, and separation of cells can be arranged into cycles capturing some fundamental features of simple colonial volvocine algae.

MATING TYPE LOCUS OF *GONIUM PECTORALE*

Takashi Hamaji[1], Yuko Mogi[2], Patrick Ferris[3], James Umen[4], Ichiro Nishii[5], Yoshiki Nishimura[1] and Hisayoshi Nozaki[2]

1. *Kyoto University, Kyoto, Japan*
2. *University of Tokyo, Tokyo, Japan*
3. *University of Arizona, AZ*
4. *Donald Danforth Plant Science Center, MO*
5. *Temasek Life Sciences Laboratory, Singapore*

The volvocine lineage is well-suited for a comparative genomic approach to the evolution of sexual dimorphism for three reasons: 1) Volvocine algae have a range of species that include

isogamous through oogamous species (Nozaki *et al*. 2000, MPE). 2) Genome sequences of oogamous *Volvox carteri* and isogamous, unicellular *Chlamydomonas reinhardtii* are available (Merchant *et al*. 2007 Science; Prochnik *et al*. 2010 Science). 3) The genetic and molecular basis of mating type differentiation in *C. reinhardtii* has been well-studied such as the mating type locus (*MT*). Key genes involved in mating type differentiation are encoded on *MT* loci in *C. reinhardtii* (Ferris and Goodenough 1994 Cell; Ferris *et al*. 2002 Genetics), the isogamous 8- or 16-celled colonial *Gonium pectorale* (Hamaji *et al*. 2008 Genetics; 2009 J. Phycol.), oogamous *Pleodorina starrii* (Nozaki *et al*. 2006 Curr. Biol.) and *V. carteri* (Ferris *et al*. 2010 Science). Because identifying key factor(s) toward oogamy requires information about *MT* of intermediate species close to oogamous organisms (Charlesworth and Charlesworth 2010 Curr. Biol.), we have sequenced BAC clones containing the *MT* region of *G. pectorale*. Draft contigs of ~500 kb from mating type *minus* and ~400 kb from mating type *plus* show that *MT* in *G. pectorale* is potentially larger than in *C. reinhardtii* . Gene composition of *MT* loci among *C. reinhardtii*, *G. pectorale* and *V. carteri* have been compared and characterized. Divergence between alleles of shared genes in the rearranged (R) domain of *MT* sheds light on their history and potential cooption into the sexual cycle.

MAT3 DIVERGENCE AFTER THE EVOLUTION OF ANISOGAMY IN THE COLONIAL VOLVOCALES

Rintaro Hiraide[1], Hiroko Kawai-Toyooka[1], Takashi Hamaji[2], James Umen[3] and Hisayoshi Nozaki[1]

1. *Dept. of Biol., University of Tokyo, Tokyo, Japan*
2. *Dept. of Botany, Kyoto University, Kyoto, Japan*
3. *Donald Danforth Plant Science Center, St. Louis, MO, USA*

The Volvocaceae are believed to be the most ideal lineage in which to study the evolution of sexual reproduction (Kirk 2006, Curr. Biol.). The transition from isogamy to anisogamy might have occurred within the Volvocaceae after the split between the *Yamagishiella* and *Eudorina* sub-lineages (Nozaki et al. 2000, MPE). For this reason, *Eudorina* plays an extremely important role in investigating the origin of male–female dimorphism. *MAT3* is a mating locus gene encoding a cell size regulatory protein that is a potential candidate responsible for the evolution of anisogamy. The male and female alleles of *MAT3* from the oogamous species *Volvox* are highly diverged from each other, but they are not diverged in isogamous *Chlamydomonas* (Ferris et al. 2010, Science). However, sequences of *MAT3* homologs have not been previously studied in the anisogamous members of the Volvocaceae. Therefore we sought to identify the *MAT3* homolog of *Eudorina.* We isolated the *MAT3* gene from male and female strains of *Eudorina* sp. and found out that there are just two base differences (including one nonsynonymous change) in the coding region (3519bp) of *MAT3* between the two sexes. These results suggest that the divergence of *MAT3* between male and female occurred after the evolution of anisogamy within the Volvocaceae. Our phylogenetic tree of MAT3 proteins also supports this scenario.

Development and Cell Differentiation (Chair: Stephen Miller)

ESTABLISHMENT OF A *VOLVOX* CHROMATIN IMMUNOPRECIPITATION (CHIP) PLATFORM TO ANALYZE THE FUNCTION OF THE MASTER CELL-FATE DETERMINATION REGULATOR REGA

Alicia D. Howard[1], Daniela Strenkert[2], Michael Schroda[2] and Stephen M. Miller[1]

1. *Dept. of Biological Sciences, University of Maryland Baltimore County, Baltimore, MD, USA*
2. *Max Planck Institute for Molecular Plant Physiology, Potsdam-Golm, Germany*

Volvox carteri possesses two cell types: large, reproductive gonidia and small, motile somatic cells that resemble *Chlamydomonas* unicells in morphology but do not divide. The *regA* gene is expressed only in somatic cells and is essential for maintaining them in a terminally differentiated state. *regA* encodes a putative transcriptional repressor (RegA) that possesses a VARL domain, which resembles the DNA-binding SAND domain of several animal and plant transcription factors. RegA is hypothesized to repress growth and reproduction in somatic cells by binding (and repressing) the promoters of nuclear-encoded chloroplast protein genes (NECPGs), since NECPG transcripts do not accumulate in wild type somatic cells but are synthesized in somatic cells of *regA* mutants. As a first step toward testing this hypothesis we have developed a chromatin immunoprecipitation (ChIP) platform for *Volvox* and are using it to assay occupancy of histones in the upstream regions of NECPGs and several other genes. We have optimized a number of experimental parameters, including DNA-protein crosslinking, chromatin shearing, antibody incubations, and real time PCR conditions. As a first test of our platform we examined occupancy of histone H3 at the *hsp70A* and control promoters under ambient and heat shock conditions. Consistent with previous results others have reported for heat shock gene promoters in other organisms, our results indicate that heat shock induces marked displacement of histones from the *hsp70A* promoter. We are now applying our ChIP protocol in a ChIP-seq experiment to determine RegA targets. Progress toward the goal of identifying these targets will be reported.

LIGHT RECEPTORS OF *VOLVOX CARTERI*

Arash Kianianmomeni[1] and Armin Hallmann[2]

1. *Institute of Biology, Experimental Biophysics, Humboldt-University of Berlin Invalidenstr., Berlin, Germany*
2. *Department of Cellular and Developmental Biology of Plants, University of Bielefeld Universitätsstr., Bielefeld, Germany*

The photosynthetic organisms like green algae of the family Volvocaceae use light receptor system to find optimal environmental conditions for photosynthesis and to avoid light damage. Many other survival processes like gene expression, protein and lipid synthesis are initiated and regulated by the light. In *Volvox carteri*, three groups of light receptors have been identified based on genome sequence database of JGI: phototropin (VcPHOT1), two

cryptochromes (VcCRYp and VcCRYa) and eight member of rhodopsin-like receptor family (Vop1 and Vop2, VchR1, VchR2, VcCop5, VcCop6, VcCop7 and VcCop8).

VcPHOT1, VcCRYp and VcCRYa are homolog to known plant blue light receptors. In contrast, there is no evidence for red light receptors, so called phytochromes, in *Volvox*. However, only VchR1 and VchR2 have been characterized as bleu light receptors and no data is available regarding to the light spectra properties of other six members of rhodopsin-like receptors.

The characterization study of *VchR1* and *VchR2* show that these two genes are extremely expressed in somatic cells of *Volvox*. The expression of *VchR1* is very high at the points of cell differentiation and release during both asexual and sexual life cycles. Moreover, the expression is very sensitive to environmental factors like light and temperature. *VchR2* is more expressed at the point of cell differentiation, especially by sexual life cycle. Since blue light is involved by regulation of sexual life cycle in green algae, *VchR2* might play a key role in sexual development of *Volvox*. The characterization of other blue light receptors indicates that their expression is regulated by cell type and developmental stages in *Volvox*.

ELEMENTAL MAPPING OF *VOLVOX* DURING OXIDATIVE STRESS

Oana Marcu[1,2], Matthew Lera[1,3], Helen Nichol[4] and Samuel Webb[5]

1. *Space Biosciences Division, NASA Ames Research Center, Moffett Field, CA, USA*
2. *Carl Sagan Center, SETI Institute, Mountain View, CA, USA*
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4. *Department of Anatomy and Cell Biology, University of Saskatchewan, SK, Canada*
5. *Stanford Synchrotron Radiation Lightsource, Stanford Linear Accelerator Center, CA, USA*

A common response of all cellular life to changes in environmental conditions is the intracellular production of reactive oxygen species (ROS). At significant levels these can damage biomolecules, yet they also act as important signaling cues that ensure adaptive responses and survival. A stable intracellular redox milieu is crucial for the structural integrity of cells and for cell fate decisions[1]. This balance can be maintained by intracellular elements (transition metals and salt ions[2,3]) that mitigate the reactivity of oxygen species.

We have shown using microprobe X-ray fluorescence imaging that in *Volvox carteri* the production of reactive oxygen species in response to heat stress correlates with the cellular transit of several elements. The presence and ratio of these elements may be responsible for the regulation of reactive oxygen species formed during heat stress[4].

The distinct signature of germ vs somatic cells in *Volvox* indicates differential accumulation of elements during development, and tests the hypothesis that intracellular ions regulate ROS and thus the downstream pathways specific to each cell type during changes in environmental conditions.

[1] Burhans, W.C. and N.H. Heintz. Free Radic Biol Med, 2009, 47(9):1282-93
[2] Daly MJ, et al., PLoSBiol, 2007, 5(4): e92. doi:10.1371/journal.pbio.0050092
[3] Kish, A., et al., Environ Microbiol, 2009. 11(5): p. 1066-78.
[4] Nedelcu, A.M., et al, Proc Biol Sci, 2004. 271(1548): p. 1591-6.

The physics of being multicellular (Chair: John Kessler)

WHY MOTILITY?

John O. Kessler
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Volvocales live in environments ranging from deep waters, quiescent or agitated, to puddles with depth of one or a few centimeters. While deep habitats present concentrations or intensities such as nutrients and illumination, ranging from marginal to optimum, shallow ones do not. Swimming occurs in all of them. "Reasons" for swimming -- getting someplace that is environmentally "better", escaping predators, improving the rate of inward-and-outward molecular transport, generation of intracolony gradients, conservation of obsolete evolved properties, or "just can't help it" -- will be discussed.

Support by DOE DEAC02-06CH11357 is gratefully acknowledged.

THE FIDELITY OF PHOTOTAXIS IN *VOLVOX CARTERI*

Knut Drescher[1,2], Raymond E. Goldstein[1] and Idan Tuval[1]

1. *Department of Applied Mathematics and Theoretical Physics, University of Cambridge*
2. *Present Address: Department of Molecular Biology, Princeton University*

Along the evolutionary path from single cells to multicellular organisms with a central nervous system are species of intermediate complexity that move in ways suggesting high-level coordination, yet have none. Instead, organisms of this type possess many autonomous cells endowed with programs that have evolved to achieve concerted responses to environmental stimuli. Here experiment and theory are used to develop a quantitative understanding of how cells of such organisms coordinate to achieve phototaxis, by using the colonial alga *Volvox carteri* as a model. It is shown that the surface somatic cells act as individuals but are orchestrated by their relative position in the spherical extracellular matrix and their common photoresponse function to achieve colony-level coordination. Analysis of models that range from the minimal to the biologically faithful shows that, because the flagellar beating displays an adaptive down-regulation in response to light, the colony needs to spin around its swimming direction and that the response kinetics and natural spinning frequency of the colony appear to be mutually tuned to give the maximum photoresponse. These models further predict that the phototactic ability decreases dramatically when the colony does not spin at its natural frequency, a result confirmed by phototaxis assays in which colony rotation was slowed by increasing the fluid viscosity.

A GENERAL ALLOMETRIC AND LIFE-HISTORY MODEL FOR THE TRANSITION TO MULTICELLULARITY AND CELLULAR DIFFERENTIATION

Cristian A. Solari[1], John O. Kessler[2] and Raymond E. Goldstein[3]

1. *CONICET Researcher, Laboratorio de Biología Comparada de Protistas, Departamento de Biodiversidad y Biología Experimental (FCEyN), Universidad de Buenos Aires, Buenos Aires, Argentina*
2. *Department of Physics, University of Arizona, Tucson, AZ, USA*
3. *Department of Applied Mathematics and Theoretical Physics, University of Cambridge, Cambridge, UK*

The transition from unicellular, to colonial, to larger multicellular organisms has benefits, costs, and requirements. Here we present a simple model that explains the dynamics involved in the unicellular-multicellular transition using life-history theory and allometry. We model the two fitness components (fecundity and viability) and compare the fitness of hypothetical colonies of different sizes with varying degrees of cellular differentiation to try to understand the general principles that underlie the evolution of multicellularity. We argue that germ-soma separation evolved as a means to counteract the increasing costs and requirements of larger multicellular colonies. The model shows first that the cost of investing in soma decreases with size. Secondly, as reproduction costs increase exponentially with size for undifferentiated colonies, soma specialization can give an indirect benefit to the colony by decreasing such costs and a direct benefit by helping reproductive cells acquire resources for their metabolic needs. Thirdly, germ specialization is favored once soma has evolved and takes care of vegetative functions. Some volvocine green algae allometric relationships are used to explain the model. Our model and analysis shows that the cost of reproducing an increasingly larger group likely played an important role in the transition to multicellularity and cellular differentiation.

Evolution (Chair: Matthew Herron)

EVO-VOLVO: USING THE VOLVOCINE ALGAE TO ADDRESS EVOLUTIONARY QUESTIONS

Aurora M. Nedelcu

Department of Biology, University of New Brunswick, Fredericton, NB, Canada

"Few groups of organisms hold such a fascination for evolutionary biologists as the Volvocales. It is almost as if these algae were designed to exemplify the process of evolution" (Bell 1985). Indeed, volvocine algae have proved to be an excellent system to address questions concerned with the evolution of multicellularity, complexity, cell differentiation and development. More recently, a series of new general evolutionary questions are being investigated using this group of algae. I will discuss some of these questions (related to the evolution of sex, programmed cell death, reproductive altruism and senescence) and present our approaches to address them.

RAPID TRANSITION TOWARDS THE DIVISION OF LABOR VIA EVOLUTION OF DEVELOPMENTAL PLASTICITY

Sergey Gavrilets

Department of Ecology and Evolutionary Biology, Department of Mathematics, National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, TN, USA

A crucial step in several major evolutionary transitions is the division of labor between components of the emerging higher-level evolutionary unit. Examples include the separation of germ and soma in simple multicellular organisms, appearance of multiple cell types and organs in more complex organisms, and emergence of casts in eusocial insects. How the division of labor was achieved in the face of selfishness of lower-level units is controversial. I present a simple mathematical model describing the evolutionary emergence of the division of labor via developmental plasticity starting with a colony of undifferentiated cells and ending with completely differentiated multicellular organisms. I explore how the plausibility and the dynamics of the division of labor depend on its fitness advantage, mutation rate, costs of developmental plasticity, and the colony size. The model shows that the transition to differentiated multicellularity, which has happened many times in the history of life, can be achieved relatively easily. My approach is expandable in a number of directions including the emergence of multiple cell types, complex organs, or casts of eusocial insects.

COMPLEXITY AND INDIVIDUALITY IN THE VOLVOCINE ALGAE

Matthew D. Herron

Department of Zoology, University of British Columbia, Vancouver, BC, Canada

A single-celled protist such as *Chlamydomonas* is unambiguously an individual, as is a differentiated multicellular organism such as *Volvox*. By some criteria at least, multicellular organisms are more complex than unicellular ones. What are these criteria, and how does this increase in complexity take place? At what point during the evolution of multicellular organisms do groups of cells become individuals in their own right? I consider these questions in light of the developmental changes involved in the evolution of multicellularity in the volvocine algae.

Genomics (Chair: Bradley JSC Olson)

THE *VOLVOX* GENOME PROVIDES INSIGHTS INTO EVOLUTIONARY STRATEGIES FOR EVOLVING COMPLEXITY

Simon Prochnik[1], James Umen[2], Aurora M Nedelcu[3], Armin Hallmann[4], Stephen M Miller[5], Ichiro Nishii[6], Jeremy Schmutz[7], Jane Grimwood[7] and Daniel Rokhsar[1,8]

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Muliticellularity has evolved in half a dozen major eukaryotic groups. Outside the opisthokonts, the closely-related chlorophytes *Volvox carteri* and *Chlamydomonas reinhardtii* represent the first pair of sequenced species that span the evolution of multicellularity. Comparisons of the genome sequences and the ~15,000 predicted protein coding genes apiece reveal insights into the genetic changes that accompanied the evolution of multicellularity within the green algal lineage. A core set of nearly 2,000 genes is uniquely shared between the two chlorphyceae. Strikingly, those gene families associated with extra-cellular matrix are dramatically larger in *Volvox* than *Chlamydomonas*. These clade-specific gene families likely provided the raw materials for changes that accompanied the evolution of multicellularity, in contrast to the large-scale invention of proteins accompanying the appearance of metazoans or the signal transduction protein based evolutionary strategy for increasing complexity recently revealed by the sequencing of multicellular *Ectocarpus* (Phaeophytes). Directed genome finishing and deep transcript sequencing in both chlorophyte species has improved genome assemblies and annotations. For example the v.4 *Chlamydomonas* assembly is now chromosome-scale and 5.4 million 454 EST sequences have modified 48% of the current 17,114 gene models. These updated resources increase the resolution of genome-scale comparisons.

THE VOLVOCALES GENOME PROJECT

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The Volvocales and their unicellular relatives have long been viewed as an important model system for the evolution of multicellularity and cellular differentiation. *Chlamydomonas* and to a lesser degree *Volvox* are well developed molecular-genetic model systems, but other Volvocacean species representing important evolutionary steps toward multicellularity, have not been as well developed. The completion of the genomes of *Chlamydomonas* and *Volvox* has demonstrated that even though these organisms differ markedly in the morphology, their genomes are surprisingly similar. This suggests that the evolutionary path to multicellularity and cellular differentiation requires only a few genetics changes. With the availability of second-generation sequencing technology, the Volvocales Genome Project seeks to focus initially on sequencing the genomes of *Gonium pectorale, Eudorina elegans and Pleodorina starii.* The project goals, sequencing and annotation strategies will be presented as well as an initial analysis of the genome assemblies.

VOLVOCALEAN ORGANELLE GENOME EVOLUTION

David Roy Smith

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Some of the most diverse and unusual mitochondrial and plastid DNAs from all eukaryotes come from green algae, particularly volvocalean algae. This talk explores the organelle genome architectural diversity within the Volvocales, and green algae as whole, and uses population genetic data from model algal species, including *Volvox carteri*, to address contemporary hypothesis on genome evolution. It is argued that the genomes of green algae are fashioned by nonadaptive forces.

NEXT GENERATION TRANSCRIPTOME SEQUENCING PROVIDES INSIGHTS INTO THE GENETIC CONTROL PROGRAM FOR SEXUAL DIFFERENTIATION IN *VOLVOX CARTERI*

Sa Geng[1], Peter L. De Hoff[2], Bradley J. S. C. Olson[3], Rhitu Rai[2] and James G. Umen[1]

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Volvox carteri makes sexually dimorphic gametes with large eggs and small sperm, and does so in response to a species-specific sex-inducer protein rather than in response to –N as occurs in *Chlamydomonas* and other Volvocine genera. The *Volvox* sex determining locus, *MT*, has two haplotypes, *MTF* and *MTM,* that are significantly expanded and diverged relative to *MT+* and *MT-* in *Chlamydomonas*. We have used RNA-seq based transcriptome analysis to compare the program of sexual differentiation in *Volvox* from vegetative and sexual stages. These data identified at least five classes of autosomal genes whose expression is under control of the *MTF* and *MTM* haplotypes. These include i) genes that are regulated by sex inducer independent of gender, ii) genes that are co-regulated by both sex inducer and *MTM*, iii) genes that are coregulated by sex inducer and *MTF*, iv) genes that are

female biased in expression independent of sex inducer, and v) genes that are male-biased in expression independent of sex inducer. Class I genes are likely involved in general aspects of sexual differentiation, while class II and III genes are likely to be involved in gender-specific functions. Interestingly, the number of genes in class II (male, sex specific) is greater than in class III (female, sex specific) and matches the observation that sperm are more highly differentiated cell types than eggs. The existence of Class IV and V genes was not anticipated, but they indicate that even in their asexual phase where they are morphologically identical, *Volvox* males and females have different autosomal gene expression profiles under the control of *MTM* and *MTF*. Together these data provide the basis for deciphering the network of gene expression involved in male and female sexual differentiation in *Volvox*.

Molecular and Evolutionary Genetics (Chair: James Umen)

THE POPULATION GENETICS OF *MT*: RESOLVING THE DIVERGENCE PARADOX BETWEEN *CHLAMYDOMONAS* AND *VOLVOX MT* GENES

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Sexual reproduction in Volvocine algae coevolved with the acquisition of multicellularity. Comparative analyses of *Chlamydomonas reinhardtii* and *Volvox carteri* mating loci provided insights into how the colonial Volvocine algae might have evolved sexual dimorphism (Ferris, Olson et al, *Science* 328 p351, 2010), but also raised questions about why the *MT* locus in *Chlamyomonas* shows less divergence between haplotypes than expected (Charlesworth, *Current Biol.* 20:12 p R250, 2010). The paradox of an unexpectedly youthful-looking *MT* locus in *Chlamydomonas* might be resolved if its evolution could be observed on longer time scales than allowed by laboratory crosses. Here we have used sequencing of *MT* genes from different geographic isolates of *Chlamydomonas* to examine the dynamics of *MT* evolution in this species. Our data reveal lower than expected nucleotide diversity in *MT* genes, and strong evidence of genetic interactions between shared genes in the *plus* and *minus* haplotypes. These interactions include gene conversion within the Rearranged (R) domain and crossover recombination in the flanking regions, none of which are observed in laboratory crosses. These data resolve the age paradox for *Chlamydomonas MT* and provide a model for how shared genes in the *Chlamydomonas MT* locus remain relatively homogenous and "youthful". They also highlight the fundamentally different evolutionary trajectories of the *C. reinhardtii* and *V. carteri MT* loci.

ELUCIDATING THE ORIGINS OF THE *REGA* GENE

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Commentators often view the most significant event in the Volvocalean evolution as the appearance of a division of labor between reproductive and somatic cells that is most apparent in the largest colonials, the genus *Volvox*. Mutant searches in *V. carteri* identified only a single locus, *regA*, with a clear-cut effect on germ-soma determination: the apparent somatic cells of the mutant spheroids soon regenerate into reproductive cells, instead of undergoing cell death. The *regA* gene has been characterized (Kirk et al 1999), and shown to be a VARL (SAND) domain-containing transcription factor. A phylogenetic tree of all the predicted VARL domain genes in the *Chlamydomonas* and *Volvox* genomes has been constructed (Duncan et al. 2007) and shows that the *regA* gene is one of four paralogs whose only close *Chlamydomonas* relative is the *RLS1* VARL gene.

We are currently completing the sequence of the *regA* gene from three species closely related to *V. carteri f. nagariensis*, identified using degenerate primer PCR. All of these species set aside their germ line by unequal cleavage during embryogenesis. We are now moving to the more interesting question of whether *regA* can be identified in *Volvox* species that do not have unequal cleavage and in *Pleodorina*. Attempts to isolate regenerator mutants in *Volvox* species other than *V. carteri* are also planned.

A BROADER LOOK AT THE ORIGIN OF THE VARL GENE FAMILY

Erik R. Hanschen, Patrick Ferris, and Richard E. Michod
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One of the defining characteristics of an evolutionary transition to multicellularity is the formation of terminal cellular differentiation. The evolution of specialized somatic and germ cells is almost universally the first cellular differentiation in multicellular species, reflecting its fundamental importance in the transition to multicellular life. Due to its importance in determining cellular differentiation in volvocine algae, understanding the evolution of the *regA* gene and the VARL (*regA*-like) gene family may elucidate the role of gene duplication in the evolution of multicellularity. Previous analyses have studied the relationship of VARL genes in *Chlamydomonas reinhardtii* and *Volvox carteri*, but it is difficult to resolve the evolutionary history with just two species. We investigate the origin of the VARL gene family throughout the green algae using all available genomes. An analysis of gene architecture and gene phylogenies provides insight into the origin of the VARL domain duplications in the evolution of cellular differentiation.

NEW INSIGHTS INTO THE REGULATION OF *REGA* EXPRESSION IN *VOLVOX CARTERI*

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Although most multicellular organisms comprise one or more somatic cell lineages that do not have reproductive potential, the mechanistic basis for somatic cell differentiation is poorly understood. *Volvox carteri* is a simple multicellular organism with only two cell types: ca. 2,000 small somatic cells and up to 16 large reproductive cells. In this species, somatic cell fate is determined by *regA*—a master regulatory gene that is believed to encode a transcription factor, which represses nuclear genes coding for chloroplast proteins. *regA* is expressed only in somatic cells and its induction is thought to be strictly dependent on the size of cells at the end of embryogenesis (i.e., only cells smaller than 8um express *regA* and differentiate into somatic cells). However, the mechanism responsible for translating differences in cell size into differential *regA* expression is not known. We used a RT-qPCR approach to investigate the expression pattern of *regA* in both wild-type and regenerating somatic cells (i.e., cells that regain reproductive potential) under various experimental settings. Our data provide new insights into the regulation of *regA* expression and the mechanistic basis of somatic cell differentiation in *V. carteri*, as well as (2) the evolution of somatic cell differentiation in this group of algae.

Taxonomy and Phylogeny (Chair: Hisayoshi Nozaki)

NEW VOLVOCACEAN ALGAE PROGRESSIVELY IDENTIFIED

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The Volvocaceae includes several genera that are distinguished from one another by vegetative colonies and sexual reproduction. Since Nozaki in Nozaki and Kuroiwa (1992, Phycologia) described *Yamagishiella*, no additional genera have been described in this family. Furthermore, until recently, no new species have been described in the genus *Volvox* since Starr (1970, J. Phycol.) described *V. pocockiae*.

Our recent taxonomic studies based on the cultured material and molecular phylogenetic analyses delineated three new species in the genus *Volvox*: *V.* (sect. *Merrillosphaera*) *ovalis* Nozaki & Coleman (2011, J. Phycol.), *V.* (sect. *Volvox*) *ferrisii* Isaka et al. (2012, J. Phycol. in press) and *V.* (sect. *Volvox*) *kirkiorum* Nozaki et al. in Isaka et al. (2012, J. Phycol. in press). Each of these three species has its unique morphological attributes and distinct phylogenetic position within the Volvocaceae, but lack of living material in some described species (e. g. *V. capensis*, *V. spermatosphaera*) has still been problematic in the taxonomy of the genus *Volvox*.

Very recently, a possible new genus was found from a lake in Japan. This organism is similar to *Yamagishiell*a and *Eudorina* in having 16- or 32-celled spheroidal colonies without differentiation of somatic cells. However, it differs from *Yamagishiella* by its anisogamous sexual reproduction and from *Eudorina* in distribution of contractile vacuoles on the surface of the protoplast of vegetative cells (cf. Yamada et al. 2008, Eur. J. Phycol.). Phylogenetic analyses demonstrated that it is sister to the genus *Platydorina* within the Volvocaceae.

CRYPTIC NON-GREEN ENDOSYMBIOSIS IN THE SECONDARY PHOTOSYNTHETIC EUKARYOTES, CHLORARACHNIOPHYTA, BASED ON EXTENDED PHYLOGENETIC ANALYSES

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Chlorarachniophyta is a group of photosynthetic eukaryotes harboring secondary plastids of a distinct green algal origin. Although previous phylogenetic analyses of nuclear genes encoding Calvin cycle enzymes demonstrated the presence of genes apparently not derived from green algal endosymbionts in *Bigelowiella natans* (Chlorarachniophyta), the origins of these "non-green" genes in "green" secondary phototrophs were unclear due to the limited taxon sampling. Here, we sequenced five new phosphoribulokinase (*PRK*)genes (from one euglenophyte, two chlorarachniophytes, and two glaucophytes) and performed an extended phylogenetic analysis of the genes. Our phylogenetic analyses demonstrated that the PRK sequences from three genera of Chlorarachniophyta were placed within the red algal clade. These "non-green" affiliations were supported by the taxon-specific insertion/deletion sequences in the PRK alignment. Our results suggest that *PRK* genes may have been transferred from a "red algal" ancestor to Chlorarachniophyta before the divergence of the "green" secondary phototrophs. Similarly, the extended phylogenetic analysis of sedoheptulose-1,7-bisphosphate (*SBP*) shows the same affiliation between chlorarachniophytes and red algae.

Poster Session

P1 EMBRYONIC INVERSION IN VOLVOCINE ALGAE

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One key step in the evolution from unicellular to multicellular organisms in volvocine algae is the so called "inversion", during which embryos turn themselves right-side out. In *Volvox* inversion is essential, as at the end of the embryonic cleavage, the flagellar ends of all cells point towards the interior of the embryo rather than toward the exterior where they are needed for locomotion [1], [2]. Earlier work in *Volvox carteri* showed that this morphogenetic process is driven by cell shape changes and cell movements relative to cytoplasmic bridges. [3]. However, not much is known about the underlying mechanisms and the purpose of inversion especially in related volvocine algae with a quite simple type of inversion (e.g. *Gonium*).

In order to learn more about this morphogenetic process and its evolutionary origins, inversion in several species was analyzed by light and electron microscopy.

[1] Viamontes, G. I., Kirk D. L. 1977. Cell shape changes and the mechanism of inversion in *Volvox*. *J. Cell Biol*. 75:719-730.

[2] Hallmann, A. 2006. Morphogenesis in the family Volvocaceae: different tactics for turning an embryo right-side out. *Protist* 157:445-461.

[3] Nishii, I., S. Ogihara and D. L. Kirk. 2003. A kinesin, invA, plays an essential role in *Volvox* morphogenesis. *Cell* 113:743-753.

P2 MECHANICAL ASPECTS OF INVERSION IN *VOLVOX CARTERI*

Aurelia R. Honerkamp-Smith, Jocelyn Dunstan Escudero and Raymond E. Goldstein
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Volvox carteri embryos complete their development with a dramatic inversion of the hollow sphere of cells. This process has been extensively studied [1], and in particular, the recent work of Nishii et. al. [2,3] has shown that inversion is a two-stage process, comprising a traveling wave of microtubule and kinesin dependent cell rearrangement followed by an actin and myosin dependent contraction of the posterior half of the embryo. Our goal is to quantitatively measure the force generated by this actomyosin contraction and the elastic properties of embryonic cells in order to understand inversion from a mechanical standpoint.

[1] Kirk, D. L. 1998. Volvox: molecular-genetic origins of multicellularity and cellular differentiation. Cambridge University Press.

[2] Nishii, I., S. Ogihara and D. L. Kirk. 2003. A Kinesin, InvA, plays an essential role in *Volvox* morphogenesis. *Cell* **113**:743.

[3] Nishii, I. and S. Ogihara. 1999. Actomyosin contraction of the posterior hemisphere is required for inversion of the *Volvox* embryo. *Development* **126**:2117.

P3 PHOTOTAXIS IN THE MULTICELLULAR GREEN ALGA *VOLVOX*

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Phototaxis is essential for volvocine green algae because they need to orientate themselves to receive sufficient light for photosynthesis. We analyzed the phototactic behavior in the spheroidal, multicellular volvocine green alga *Volvox rousseletii* (Volvocales, Chlorophyta) to address the question of how a multicellular organism accomplishes phototactic swimming without any known direct communication among cells. In response to light stimuli, not only did the flagella waveform and beat frequency change, but the effective stroke was reversed. Moreover, there was a photoresponse gradient from the anterior to the posterior pole of the spheroid, and only cells of the anterior hemisphere showed an effective response. The latter caused a reverse of the fluid flow that was confined to the anterior hemisphere. The responsiveness to light is consistent with an anterior-to-posterior size gradient of eyespots. At the posterior pole, the eyespots are tiny or absent, making the corresponding cells appear to be blind. Pulsed light stimulation of an immobilized spheroid was used to simulate the light fluctuation experienced by a rotating spheroid during phototaxis. The results demonstrated that in free-swimming spheroids, only those cells of the anterior hemisphere that face toward the light source reverse the beating direction in the presence of illumination; this behavior results in phototactic turning. On the basis of our results, we developed a mechanistic model that predicts the phototactic behavior in *V. rousseletii*. Our results also indicate how recently evolved multicellular organisms adapted the phototactic capabilities of their unicellular ancestors to multicellular life.

P4 ANALYSIS OF VARL DOMAIN EQUIVALENCY AMONG THE REGA-GROUP VARL PROTEINS.

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Somatic cell fate in *Volvox carteri* is controlled by RegA, a putative transcription factor that shares a conserved domain (the VARL domain) with 13 other *V. carteri* and 12 *Chlamydomonas reinhardtii* proteins known as Rls (*V. carteri*) and RLS (*C. reinhardtii*) proteins. The VARL domain is related to the SAND domain, which in certain animal proteins has been shown to have DNA-binding and protein-binding activity. To determine whether the VARL domains of the Rls/RLS proteins most closely related to RegA (the RegA-group VARL proteins) might be functionally equivalent to that of RegA, we made chimeric *regA* genes encoding proteins with VARL domains from five different Rls/RLS proteins and tested their ability to rescue the phenotype of a *regA* mutant strain. Our results provide insights into the functional divergence of these VARL domains and into the evolution of the RegA-group proteins.

P5 ABUNDANCE VARIATION OF VOLVOCALES IN RESPONSE TO TEMPERATURE CHANGE

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Temperatures are expected to increase by approximately 2-4.5°C over the next 100 years. Being able to understand the effects of this change on abundance is of high importance. Although physiologists have a well-developed theory for how the intrinsic rate of increase (r) changes with temperature (T), r has little predictive power about outcomes in competitive systems, and most populations do not experience exponential growth; they level off to a carrying capacity (K) or a stochastic equilibrium (N*). In short, the physiological predictions about r do not necessarily translate into predictions about K or N*. As far back as 1934, Gause suggested that N* shows systematic patterns as a function of T, but this has received little follow up work. To increase our scarce knowledge on how abundance responds to temperature we developed microcosm experiments with the volvocine green algae as a model system. We propose to measure in semi-continuous cultures r and N* as a function of T in single species systems, and will extend the experiments to multi-species competitive systems. r and N* was estimated as function of number of cells and chlorophyll content. Preliminary results of *Chlamydomonas reinhardtii* and *Gonium pectorale* show that these organisms follow patterns similar to the ones measured by Gause. When analyzing N* vs. r, *Gonium* shows a strong positive correlation in number of cells, but there is no clear correlation in *Chlamydomonas*. Volvocales characteristics allow studying differences in size and complexity in response to temperature.

P6 DEVELOPMENTAL RESPONSE OF *V. CARTERI* TO NUTRIENT DEPRIVATION

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Phosphorus, sulfur, and light are essential for the development and growth of almost all photosynthetic organisms. While the effects of nutrient and light limitation on growth and development have been well studied in some green species, they are not well documented for *Volvox carteri*. To this end we are analyzing the response of *V. carteri* to deprivation of light, phosphorus, and sulfur to determine how and when growth and development are affected by these environmental perturbations. We cultured *V. carteri* in the absence of light, phosphorus, and/or sulfur and documented the effect on its growth and development over the course of several generations. The effects of light deprivation were obvious within 24 hours; adult spheroids did not expand after juvenile somatic cell differentiation, and juveniles failed to expand after hatching. Surprisingly, phosphorus-starved individuals developed normally for nearly two life cycles to produce nearly-normal looking young adults in the second generation, but the gonidia of these adults were aberrantly condensed and failed to undergo embryogenesis. The development of sulfur-deprived individuals also appeared nearly normal into the second generation, but unlike the phosphorus-starved individuals, many gonidia of

the young adults of that generation remained arrested in an uncondensed state, and the somatic cells of many individuals became enlarged. Individuals grown without both phosphorus and sulfur were affected mid-way through the second life cycle; while the first-generation adult spheroids contained gonidia that completed embryogenesis, their juveniles expanded only slightly and the gonidia within those juveniles remained small and became moribund. Interestingly, under all of the starvation conditions analyzed, most spheroids continued to swim throughout the course of the time study. These studies will be used to complement expression analyses for genes suspected of mediating these deprivation responses and analyses on cell viability. Ultimately our goal is to better understand the effect of the environment on *V. carteri* development, and to better understand how the interplay between environment and genetics shaped Volvocine lineage evolution.

P7 EVOLUTION OF MULTICELLUALRITY AND INDIVIDUALITY IN THE VOLVOCINE GREEN ALGAE

Richard E. Michod

The main question addressed in our laboratory is: How and why do groups of individuals evolve into new kinds of individuals? A basic hypothesis we are considering is that multicellular individuals originated as cell groups and that fitness trade-offs drove the transition of a cell group into a multicellular individual. The basic idea is that fitness depends on both viability and fecundity. These components trade-off with each other, traits that increase one component usually decrease the other. Groups may break through these constraints when cells specialize (i.e., division of labor). However, cells that specialize at soma are reproductive altruists. How can altruism evolve? Kin selection is one answer. In the volvocine algae all groups are kin, however soma only evolves in the larger species. How & why does soma and germ (division of labor) evolve? Once germ & soma evolves, the group is indivisible, it has become a new individual. The poster presents an overview of some projects in our lab concerning these topics. The PI is indicated for each project.

P8 REGA GENE CLONNING FROM SEVERAL VOLVOX SPECIES AND CHARACTERIZATION OF REGA IN A *V. CARTERI WEISMANNIA* REGA MUTANT

Qike Li, Patrick Ferris, Pierre Durand, Richard E. Michod

One of the most basic distinctions between cell types is the one between potentially immortal cells of the germ line and the mortal cells of somatic tissues, i.e. G-S differentiation. The evolution of soma was a critical step in the evolution of complex body plans and the major radiations of multicellular life. The VARL (volvocine algal *regA*-like) gene family plays a central role in G-S differentiation in the volvocine algae. Here we have used genomic PCR with degenerate primers and inverse PCR to clone *regA* genes from various *Volvox* species. In addition, we cloned the *regA* gene from a *V.carteri weismannia* regenerator mutant and located an insert in intron 5.

P9 COOPERATION AND CONFLICT IN THE EVOLUTION OF COMPLEXITY

Richard E. Michod

The world is a very social place, what we call individuals are really societies, that is, groups of cooperating individuals. Cooperation benefits the group, yet it costs the individuals who help others. Cooperation underlies complexity and drives the emergence of new kinds of individuals during the evolutionary process. Cooperation just doesn't happen; however, there is a short term temptation to cheat leading to the tragedy of the commons. Cheating must be controlled through conflict mediation, so as to avoid the tragedy of the commons. There is a cycle of cooperation-conflict-conflict mediation which underlies the hierarchy of life and the emergence of complexity and new kinds of individuals. Groups can evolve into new kinds of individuals; this is called an evolutionary transition in individuality. Volvocine green algae illustrate the roles of cooperation and conflict in the evolution of complexity.

P10 CELL TYPE ALLOCATION AND VARIABILITY IN DIVERSE *VOLVOX* SPECIES

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Volvox (Chlorophyta) is a model system for studying the origins of cellular differentiation and allocation to distinct cell types, yet within-species patterns of cell-type allocation have not been thoroughly characterized. Additionally, the extent to which morphological and developmental differences among *Volvox* species reflect adaptive differences in life history strategy is poorly understood. Because cell-type allocation is a major aspect of life history strategies, we looked for connections between developmental features and cell-type allocation patterns in six diverse species of *Volvox*: *V. africanus*, *V. aureus*, *V. carteri* f. *weismannia*, *V. rousseletii*, *V. spermatosphaera*, and *V. tertius*. We found that somatic cell number and gonidial (asexual reproductive) cell number are positively correlated among individuals within a species. Species in this study were similar with respect to the slope of the relationship between log-transformed somatic cell number and gonidial cell number. By contrast, species differed substantially with respect to the number of somatic cells per gonidial cell. Among-species differences were also observed in the variability of gonidial cell number, and the overall level of variability in gonidial cell number appears to be high compared to similar data in more complex organisms. These data reveal little correspondence between cell-type allocation patterns and major developmental differences among species, as currently understood. Our results suggest avenues of future research, highlighting the need for a refined understanding of the ecological context in which developmentally diverse species of *Volvox* evolved.

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